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## Internal Structures in the Early Whorls of Mesozoic Ammonites

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### ABSTRACT

The first few septa and associated structures in the early whorls of Mesozoic ammonites were studied in a number of genera including *Quenstedtoceras*, *Kosmoceras*, *Euhoplites*, *Hypacanthoplites*, *Baculites*, and *Scaphites* and its related genera. Exceptionally well-preserved specimens with little obscuring matrix inside permitted observations of the spatial arrangement of the first few septa and were supplemented by sections polished parallel to the median plane. Our observations indicate that:

1. The proseptum is a single structure and does not consist of two septa. Prismatic attachment deposits of the caecum and siphuncle occur around the proseptal opening.

2. In all genera except *Quenstedtoceras*, the second septum is moderately distant from the proseptum and, in median section, is slightly convex,

not concave, toward the aperture. In *Quenstedtoceras*, however, the second septum grows dorsally into the proseptum and is only conspicuous on the venter. These relationships are also expressed in the shape and spacing of the corresponding sutures on steinkerns of the initial whorls.

3. In all genera in which the original shell structure was preserved, the second septum is nacreous, not prismatic. Therefore, in agreement with Drushchits and Khiami (1970), we prefer the simpler terms second septum and third septum for primary septum and nacreoseptum, respectively.

4. The development of a prismatic attachment ridge at the base of the proseptum, dorsal muscle scars just adoral of each septum, and wrinkles in the proseptum and prosiphonal attachment sheets support the model of early ammonite ontogeny proposed by Bandel (1982).

### INTRODUCTION

The early whorls of ammonite shells feature a complex arrangement of internal elements (Hyatt, 1894; Grandjean, 1910; Schindewolf, 1954; Arkell, 1957). Recently, Tanabe et al. (1979) studied these elements

for their taxonomic utility and identified coherent clusters of character states that represent different ammonite groups that are established mainly on the basis of other characters. These elements have also been

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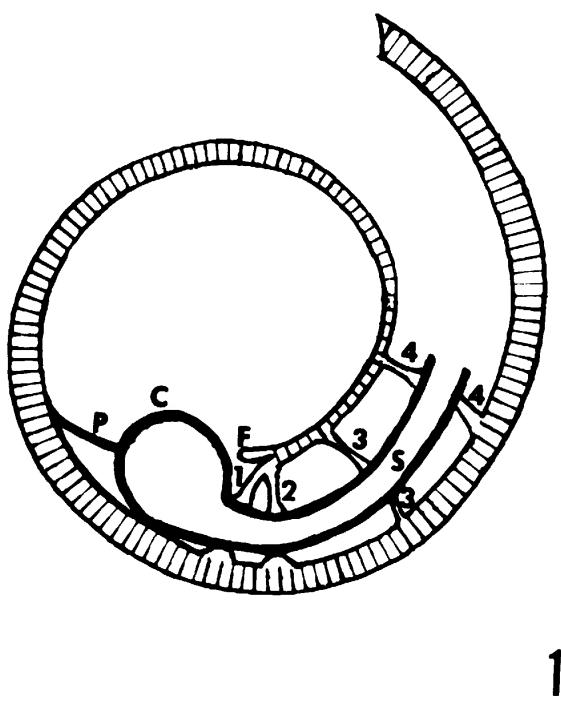


FIG. 1. Generalized median cross section of the protoconch and first whorl after Erben, Flajs, and Siehl (1969) shows the caecum (C), prosiphon (P), siphuncle (S), flange (F), proseptum (1), second (2), third (3), and fourth (4) septa.

studied to elucidate the ontogenetic development and functional morphology of newly hatched ammonites (Bandel, 1982).

As shown in a generalized median section (fig. 1 after Erben, Flajs, and Siehl, 1969), these morphologic features consist of the initial chamber or protoconch, the inner lip or flange, the first septum or proseptum, the second septum or primary septum, the third septum, the beginning of the siphuncle or caecum, the attachment sheets of the caecum or prosiphons, and the siphuncle.

Although these basic features are well established, they cannot always be clearly identified because of variation in their shape and position. Identification is especially difficult in median sections in which a three-dimensional perspective is lacking. In this paper we report the results of our investigations on the internal elements in several ammonite specimens free of interior matrix. These results permit us to address a number of issues that have been raised in the literature.

1. The presence of two prosepta. Arkell (1957) cites Grandjean (1910) as describing two prosepta although the first definite reference to this construction appears in Böhmers' (1936) and Miller and Unklesbay's (1943) studies of Permian ammonites. Schindewolf (1954) disagreed with their description, but recently, Drushchits and Doguzhayeva (1974) and Tanabe, Fukuda, and Obata (1980) reported two prosepta in Mesozoic ammonites.

2. The relationship between the proseptum and second septum. Schindewolf (1928, 1929, 1951, 1954) called the first and second septa the proseptum and primary septum, respectively, to emphasize their difference in shape. According to Erben, Flajs, and Siehl (1969), these two septa commonly lie very close together and, in median section, run straight or concave toward the aperture as compared to later septa. However, Dauphin (1975) noted an exception to this rule, which she interpreted as an anomaly of growth.

To further complicate matters, the first two septa, like all succeeding septa, display prismatic deposits which attach the septa to the siphuncle. These deposits, referred to as false septal necks (Birkelund and Hansen, 1974), cuffs (Drushchits, Doguzhayeva, and Lominadze, 1977), auxiliary deposits (Kulicki, 1979), and prismatic attachment deposits (Bandel, 1982), are conspicuous on larger septa. However, their distribution on the first few septa is sometimes confusing and may obscure the identification of these septa and their spatial relationships.

3. The structure of the second septum. The prismatic structure of the first septum is well established, but the structure of the second septum is in dispute. Erben, Flajs, and Siehl (1969) enumerated 16 ammonite genera in which the second septum was prismatic, including *Quenstedtoceras*, *Acanthoscaphites*, and *Discoscaphites*. The first nacreous septum they observed was the third septum, and they, therefore, called it the first nacreoseptum. However, Birkelund and Hansen (1974), Kulicki (1979), and Bandel (1982) have since noted that the second septum is nacreous in many ammonites.

4. The first few sutures. The prosuture and subsequent sutures form at the contact between the corresponding septa and the outer

TABLE 1  
Age and Locality of Species Studied

Species	Age (Formation)	Locality	Previous SEM Studies
<i>Discoscaphites conradi</i> (Morton)	Maastrichtian (Fox Hills Formation)	South Dakota	Bandel et al., 1982
<i>Hoploscaphites nicolleti</i> (Owen)	Maastrichtian (Fox Hills Formation)	South Dakota	Erben et al., 1969
<i>Hoploscaphites</i> sp.	Campanian	South Dakota	Bandel et al., 1982
<i>Clioscaphites vermiciformis</i> (Meek and Hayden)	Santonian (Marias River Shale)	Montana	Landman, 1982a
<i>Pteroscapheites auriculatus</i> (Cobban)	Coniacian (Marias River Shale)	Montana	Bandel et al., 1982
<i>Scaphites preventricosus</i> Cobban	Coniacian (Marias River Shale)	Montana	Landman, 1982a
<i>Scaphites</i> sp.	Coniacian-Campanian	Nugssuaq, West Greenland	Birkelund and Hansen, 1974
<sup>a</sup> <i>Scaphites cf. whitfieldi</i> Cobban	Turonian (Carlile Shale)	South Dakota	Bandel et al., 1982
<i>Scaphites whitfieldi</i> Cobban	Turonian (Carlile Shale)	South Dakota	Landman, 1982a
<i>Scaphites larvaeformis</i> Meek and Hayden	Turonian (Carlile Shale)	South Dakota	Bandel et al., 1982
<sup>a</sup> <i>Baculites</i> sp. juveniles	Santonian (Marias River Shale; Cody Shale)	Montana	Landman, 1982b
<sup>a</sup> <i>Euhoplites</i> sp.	Albian (Lower Gault)	Folkestone, England	
<sup>a</sup> <i>Hypacanthoplites</i> sp.	Aptian	Algermissen, Germany	
<sup>a</sup> <i>Quenstedtoceras</i> sp.	Callovian (erratic boulders)	Lukow, Poland	
<sup>a</sup> <i>Kosmoceras</i> sp.	Callovian (erratic boulders)	Lukow, Poland	Erben et al., 1969
			Blind, 1979
			Kulicki, 1979
			Bandel, 1982
			Erben et al., 1969
			Kulicki, 1979

<sup>a</sup> Exceptional preservation.

wall. How do the shape and spacing of these early sutures reflect the spatial relationships of the first few septa?

#### MATERIAL AND METHODS

Resolving these issues requires well-preserved material retaining the original shell for sectioning. However, study of the three-dimensional geometry of the internal elements further requires specimens free of any interior matrix. Such preservation is rare but has been discovered in a variety of Mesozoic ammonites which, thereby, dictated the taxonomic composition of the material studied (tables 1, 2). These ammonites fell into two suborders, Ammonitina and Ancyloceratina (table 2). *Kosmoceras* and *Quenstedtoceras* belong to two separate families in the same super-

family within Ammonitina. *Euhoplites* belongs to another superfamily within the same suborder. *Hypacanthoplites*, *Baculites*, and *Scaphites* and its allied genera represent three different superfamilies within Ancyloceratina. Altogether, these genera range geologically from Callovian to Maastrichtian and geographically from western Europe to western Greenland to the Western Interior of North America. Many of these genera have previously been studied with scanning electron microscopy (SEM; table 1).

Specimens free of obscuring matrix were dissected and viewed under SEM. Subsequent removal of parts of the shell sometimes exposed new features and such specimens were reexamined. Specimens filled with matrix, on the other hand, were embedded in epoxy and ground and polished parallel to

TABLE 2  
Taxonomic Distribution of Species Studied

Suborder Ammonitina
Superfamily Stephanocerataceae
Family Kosmoceratidae
Subfamily Kosmoceratiniae
<i>Kosmoceras</i> sp.
Family Cardioceratidae
Subfamily Cardioceratiniae
<i>Quenstedtoceras</i> sp.
Superfamily Hoplitaceae
Family Hoplitidae
Subfamily Hoplitiniae
<i>Euhoplitites</i> sp.
Suborder Ancyloceratina
Superfamily Deshayesitaceae
Family Parahoplitidae
Subfamily Acanthohoplitiniae
<i>Hypacanthoplites</i> sp.
Superfamily Turrilitaceae
Family Baculitidae
<i>Baculites</i> sp.
Superfamily Scaphitaceae
Family Scaphitidae
Subfamily Scaphitiniae
<i>Scaphites whitfieldi</i> Cobban
<i>Scaphites larvaformis</i> Meek and Hayden
<i>Scaphites preventricosus</i> Cobban
<i>Pteroscapheites auriculatus</i> (Cobban)
<i>Clioscaphites vermiformis</i> (Meek and Hayden)
<i>Hoploscapheites nicolleti</i> (Owen)
<i>Discoscapheites conradi</i> (Morton)

the median plane. The polished surfaces were etched with EDTA for several minutes to prepare acetate peels. Peels were coated with gold and viewed under SEM. All illustrated specimens are either in the collections of the American Museum of Natural History (AMNH) or the Yale Peabody Museum (YPM). Scale bars in all illustrations are 40  $\mu\text{m}$  unless noted otherwise.

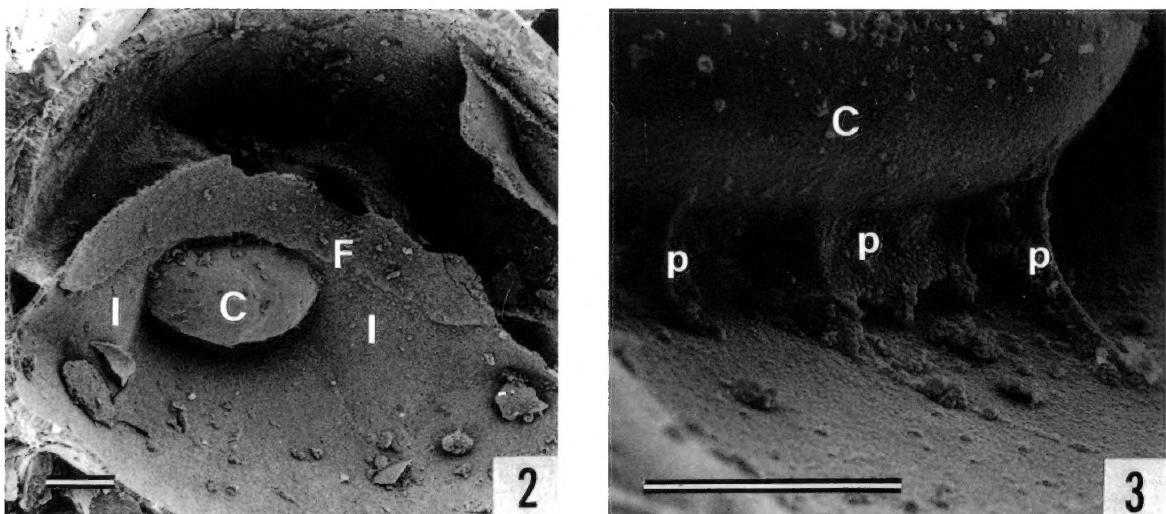
## RESULTS

1. *Scaphites*, *Clioscaphites*, *Pteroscapheites*, *Hoploscapheites*, and *Discoscapheites* (figs. 2–15). In all these genera, the protoconch typically features a bulbous caecum which is attached to the wall of the first chamber by short prosiphonal sheets. The proseptum forms a median saddle. The proximal end of the initial chamber consists of a projecting flange above the caecum (figs. 2, 3).

The proseptum, the proseptal opening, and the second septum are further exposed in specimens in which the caecum is removed or not preserved (figs. 4–7). Such specimens reveal a necklike attachment of the proseptum which develops near the median plane and curves in an adoral direction. This structure rides ventrally on the wall of the first whorl and precedes the second septum.

The interrelationships of these features are displayed in a series of sections prepared parallel to the median plane from a single specimen (figs. 8–13). In the most lateral section (fig. 8), the proseptum stretches as a single, unbroken structure. The flange projects above it but only becomes conspicuous toward the median plane. In this and all subsequent sections, the second septum is adoral of the proseptum (to the right in these figures) and separate from it. In the next most-lateral section (fig. 9), the proseptum develops a local thickening where its necklike attachment begins to emerge. These two features subsequently separate (fig. 10) except at their dorsal and ventral ends. In the next section (fig. 11), the proseptum opens up to expose part of the caecum. The opening of the proseptum is wider than that of its necklike attachment which, therefore, is still unbroken at this point. In the last section (fig. 12), however, both these structures open up onto the siphuncle and caecum and are only conspicuous just below the flange. Ventrally, the proseptum and its necklike attachment are inconspicuous and spaced moderately far apart. They have diverged on the venter as the median plane was approached. Additional prismatic deposits connect the proseptum and its necklike attachment to the siphuncle and caecum and are especially well developed on the dorsal side (figs. 12, 13). The second septum is adoral and slightly convex toward the aperture.

The proseptum and its necklike attachment are prismatic in microstructure and display a groove around their openings (fig. 6). The necklike attachment of the proseptum develops near the median plane where it surrounds the distal end of the caecum and forms an adorally directed bend on the venter. The second septum is nacreous and separate from the proseptum. The two septa only intersect on the extreme lateral margins (fig. 4).



FIGS. 2-3. *Scaphites* cf. *whitfieldi*. 2. *Scaphites* cf. *whitfieldi* (AMNH 42899). Interior of the protoconch reveals the proseptum (I), flange (F), and caecum (C). 3. *Scaphites* cf. *whitfieldi* (YPM 6239). Thin prosiphonal sheets (p) attach the caecum (C) to the protoconch wall.

These relationships are supported by observations of the corresponding sutures on steinkerns of the initial whorls (figs. 14, 15). The prosuture is angustellate, but the necklike attachment of the proseptum forms a small saddle, which is superimposed above the ventral saddle of the prosuture. The actual second suture is distinctly separated from the prosuture and the two only join on the extreme lateral margins. This arrangement has been observed in *Scaphites* and all its related genera studied from North America and Greenland.

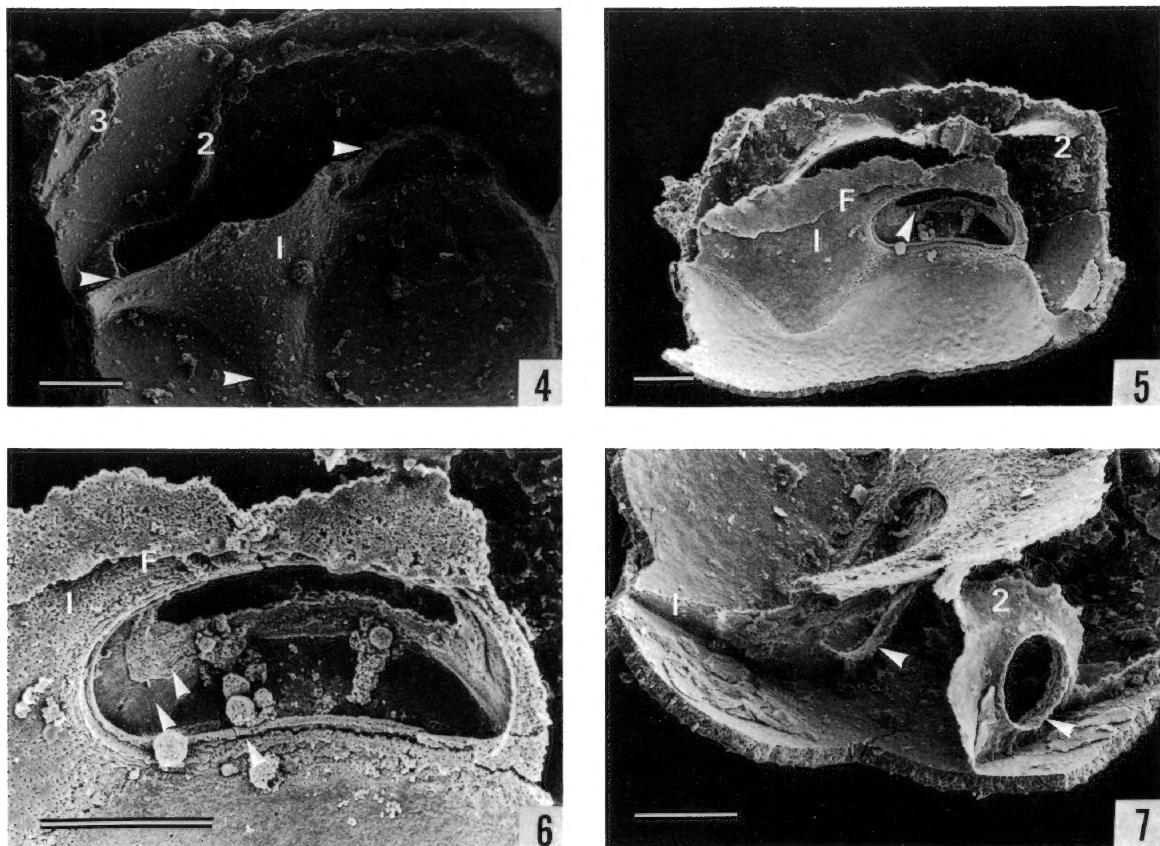
2. *Baculites* (figs. 16-26). Protoconchs of this genus in which the caecum was not preserved reveal the flange, proseptum, and pro-septal opening (figs. 16, 17). The proseptum displays wrinkles on its lateral lobes and on its extension below the flange (figs. 18, 21). A ridge occurs at the attachment of the proseptum to the protoconch wall (fig. 18). In the pro-septal opening, a short necklike attachment of the proseptum occurs which forms a small adoral bend on the venter (figs. 17, 19, 20). The second septum lies at a moderate distance from the proseptum (fig. 19).

A series of sections prepared parallel to the median plane further reveal the geometry of the first two septa (figs. 22-25). In the most lateral section (fig. 22), the proseptum

stretches undivided and the flange projects above it. The second septum is separate and adoral (to the right in these figures). In the next section (fig. 23), the necklike attachment of the proseptum begins to emerge. Nearer the median plane (fig. 24), both the proseptum and its necklike attachment open up onto the caecum and siphuncle, although these features are not preserved here. The second septum is still unbroken at this point. A final median section (fig. 25) reveals the first two septa, the necklike attachment of the proseptum, and the septal neck of the second septum. The second septum is slightly convex toward the aperture.

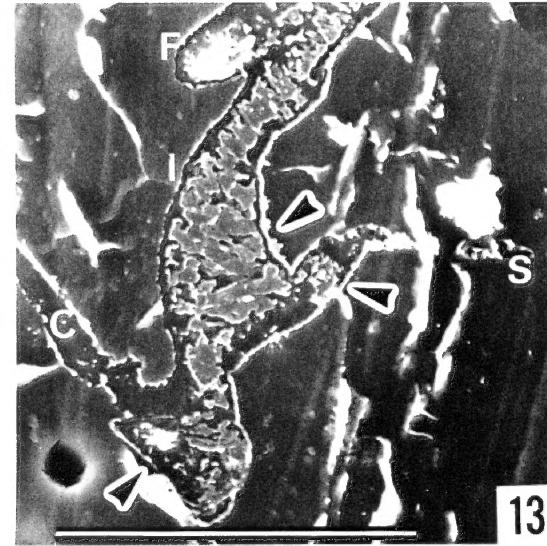
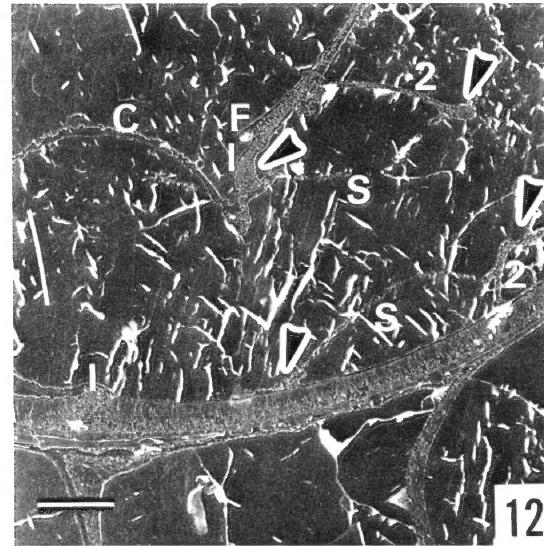
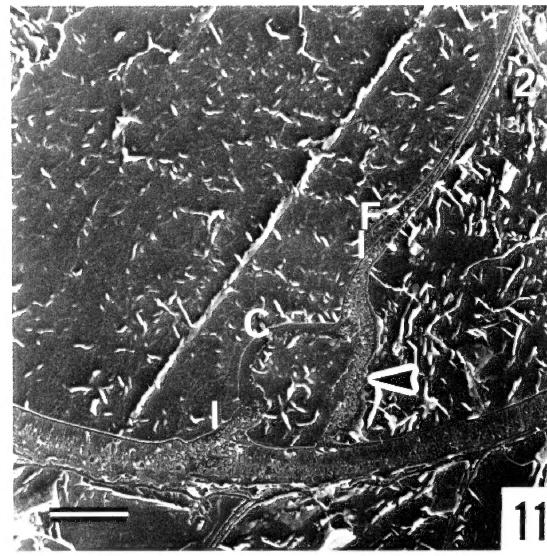
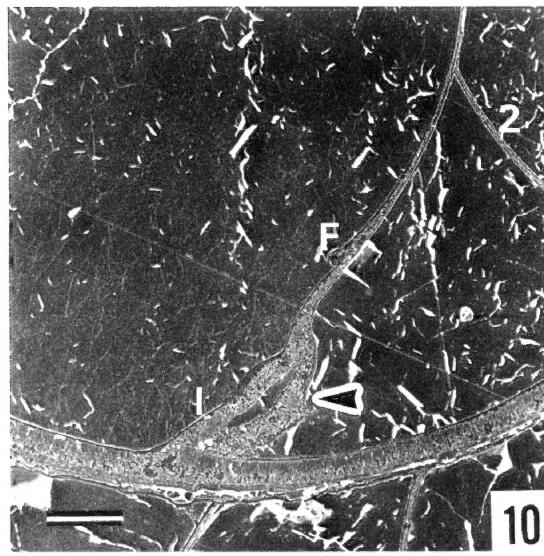
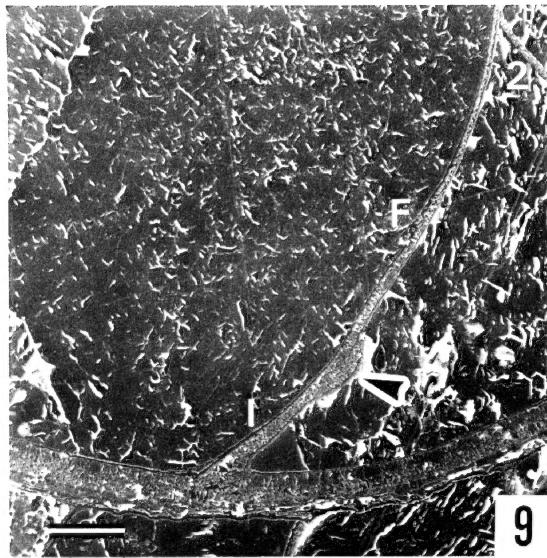
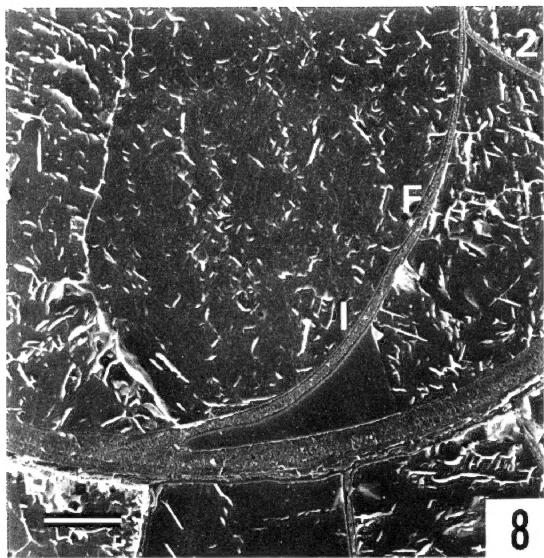
The proseptum and its necklike attachment are prismatic. The second septum is nacreous and displays a prochoanitic septal neck which is especially well developed on the ventral side (fig. 25). Examination of steinkerns of the initial whorls reveals that the short necklike attachment of the proseptum is not expressed as a saddle. The prosuture and second suture are distinct and moderately far apart (fig. 26).

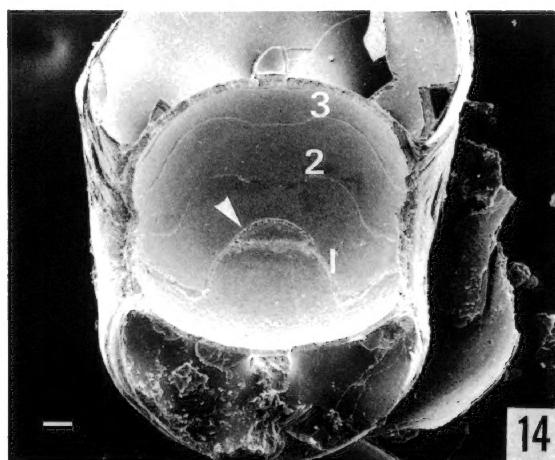
3. *Euhoplites* (figs. 27-34). A single protoconch of this genus reveals a caecum with a spatulate prosiphonal attachment sheet, a proseptum, and a flange projecting above the caecum (fig. 27). The caecum also displays



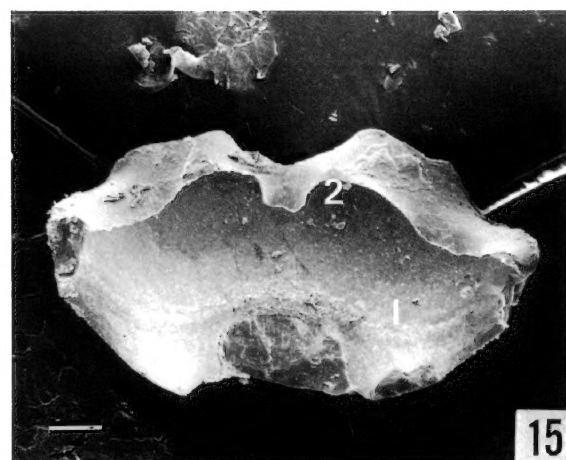
Figs. 4–7. *Scaphites* cf. *whitfieldi*. 4. *Scaphites* cf. *whitfieldi* (YPM 6240). View into the interior of the protoconch and first whorl reveals the proseptum (1), necklike attachment of the proseptum (upper arrow), and ventral traces of the second (2) and third (3) septa. The second septum only intersects the proseptum at the extreme lateral margins (middle arrow). A prismatic ridge occurs at the base of the proseptum (lower arrow). The caecum and siphuncle are not preserved. 5. *Scaphites* cf. *whitfieldi* (AMNH 42900). Interior of the protoconch and first whorl shows the proseptum (1), flange (F), opening of the proseptum with its necklike attachment (arrow), and second septum (2). 6. *Scaphites* cf. *whitfieldi* (AMNH 42900). Close-up of the specimen in figure 5 reveals the proseptum (1), flange (F), and necklike attachment of the proseptum (middle arrow). Additional prismatic attachment deposits of the siphuncle (upper arrow) occur on the necklike attachment of the proseptum. A groove (lower arrow) occurs around the opening of the proseptum. 7. *Scaphites* cf. *whitfieldi* (AMNH 42901). View from the first whorl looking back into the protoconch across the proseptum (1) and second septum (2) reveals the necklike attachment of the proseptum (left arrow) and the prochoanitic septal neck of the second septum (right arrow).

→  
 Figs. 8–13. *Scaphites preventricosus* (AMNH 42902). Five serial sections of the same specimen prepared parallel to the median plane (scale bar 20  $\mu$ m). 8. The most lateral section shows the proseptum (1), flange (F), and second septum (2). 9. In the next most-lateral section, the necklike attachment of the proseptum (arrow) begins to emerge. 10. In this section, the proseptum (1) and its necklike attachment (arrow) display an incipient separation. 11. In the next to last section, the proseptum (1) has opened to reveal part of the caecum (C). The necklike attachment of the proseptum (arrow) is still unbroken. 12. The final median section shows the caecum (C), flange (F), proseptum (1), necklike attachment of the proseptum (left arrows), siphuncle (S), and second septum (2) with its septal neck (right arrows). Additional prismatic attachment deposits of the siphuncle and caecum occur at the septal openings. 13. Close-up of the dorsal part of the proseptum (1) in figure 12 reveals the flange (F), necklike attachment of the proseptum (upper arrow), caecum (C), siphuncle (S), and additional prismatic attachment deposits of the caecum and siphuncle (lower arrows).





14



15

Figs. 14–15. *Scaphites* cf. *whitfieldi*. 14. *Scaphites* cf. *whitfieldi* (AMNH 42903). Ventral view of the prosuture (1), second suture (2), and third suture (3). The saddle (arrow) formed by the necklike attachment of the proseptum is superimposed above the median saddle of the prosuture. 15. *Scaphites* cf. *whitfieldi* (AMNH 42904). Dorsal view of a steinkern shows that the prosuture (1) and second suture (2) are distinctly separated.

delicate prosiphonal strands attaching it to the protoconch wall (fig. 29). Removal of the dorsal shell further exposes the proseptum and second septum and reveals that these two septa are distinct both ventrally and dorsally and are a moderate distance apart (figs. 28, 30). On the interior surface of the dorsal shell, muscle scars appear adoral of the septal lobes (figs. 31, 32). The muscle field adoral of the proseptum is elongate. It may consist of a pair of scars, although subsequent scars are single.

The proseptum is prismatic in contrast to the second and all later septa which are nacreous. All septa show outer layers of a homogeneous structure which originally may have been organic (figs. 33, 34).

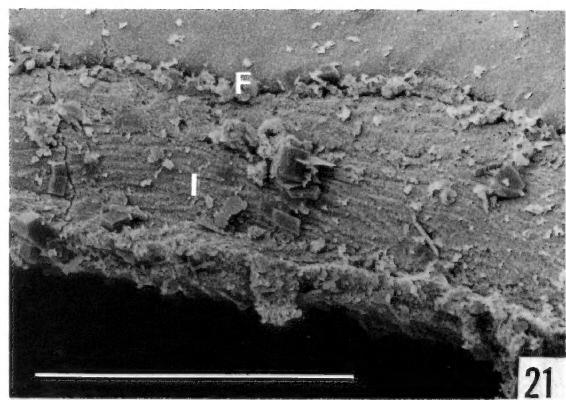
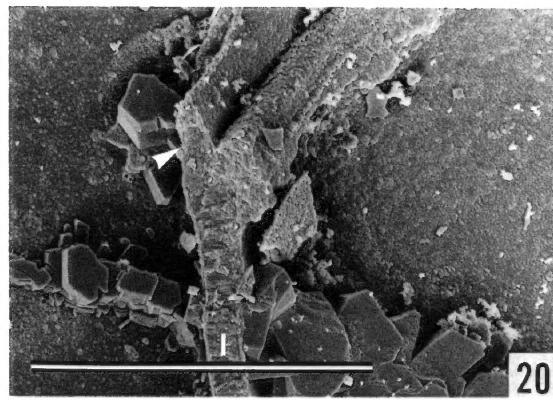
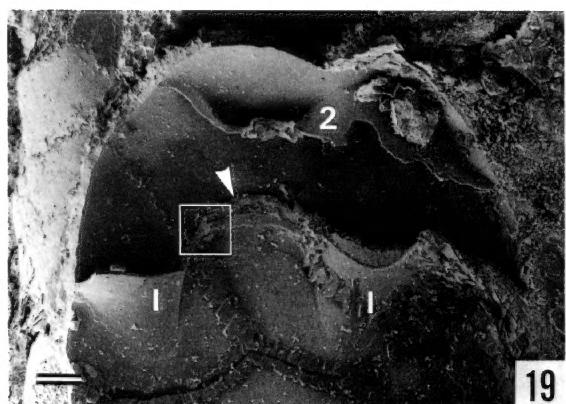
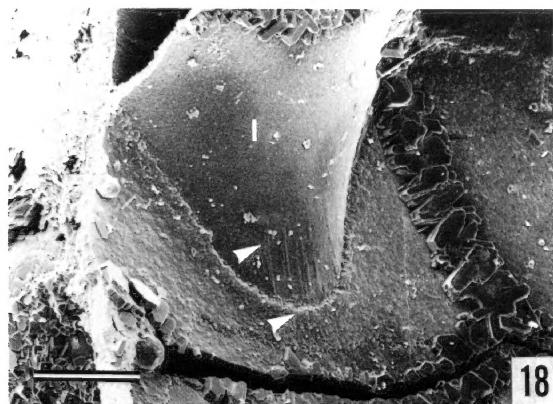
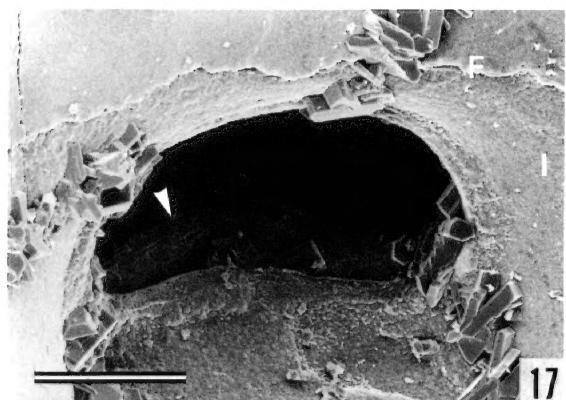
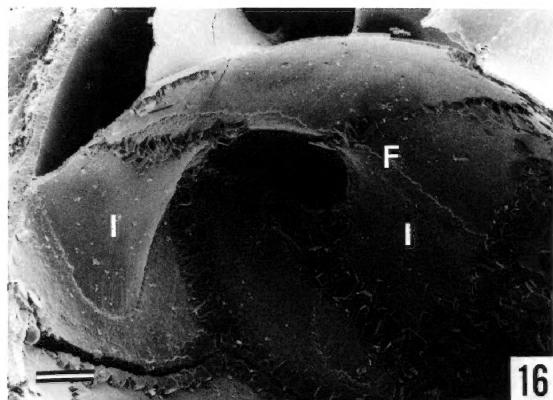
4. *Hypacanthoplites* (figs. 35–42). The protoconch, caecum, flange, and prosiphonal attachment sheets of this genus are exposed in several specimens free of matrix (figs. 35–38). The prosiphonal sheets typically consist of broad bands with shorter attachment threads (figs. 35, 37). Variation in the shape of these features may represent species-specific or individual differences. Specimens without the caecum preserved reveal the opening of the proseptum and the spacing of subsequent septa (figs. 38–42). Around the proseptal opening we observe a structure which is either

a furrow or a siphuncular attachment deposit (figs. 38, 40, 42). This feature is not nearly as well developed, however, as in *Baculites* and *Scaphites* and its related genera. The second septum is a moderate distance apart from the proseptum and in the median plane rests dorsally on the wall of the protoconch and not on the proseptum (figs. 41, 42).

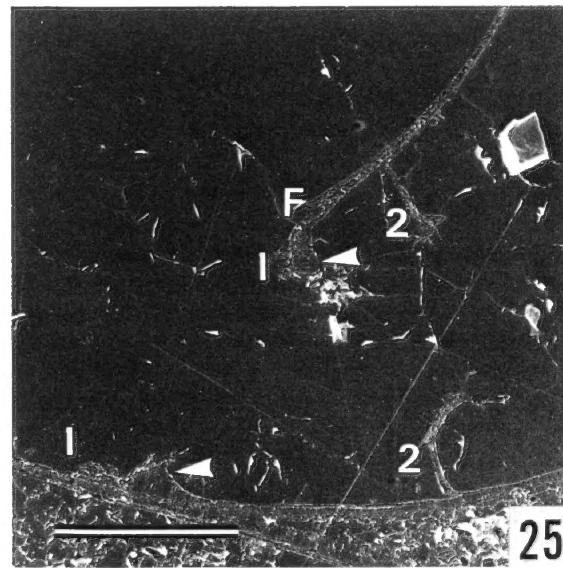
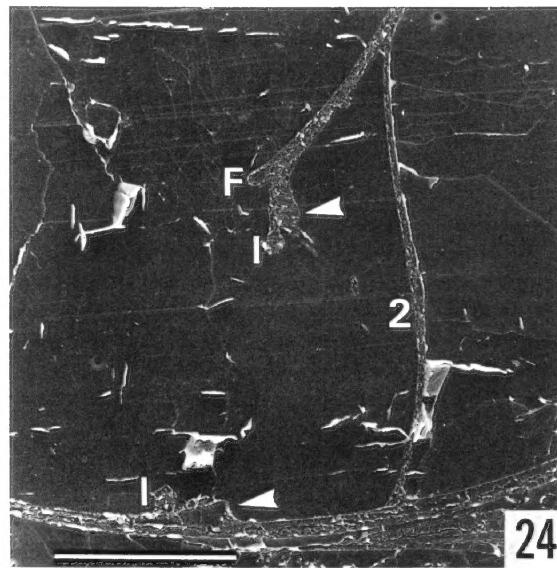
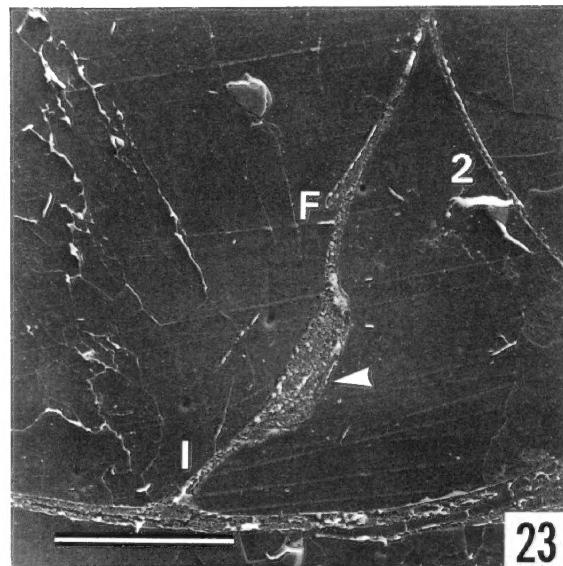
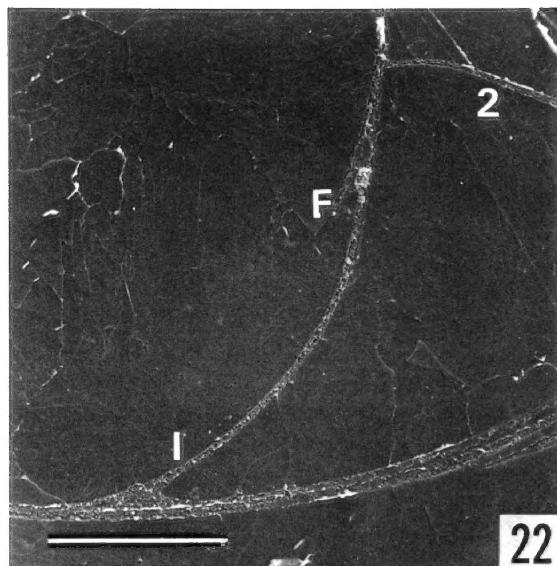
5. *Quenstedtoceras* (figs. 43–59). Protoconchs of this genus free of matrix reveal the proseptum, flange, and caecum (figs. 43–45). The caecum rests in the median saddle of the proseptum and is attached to the walls of the protoconch by prosiphonal sheets displaying wrinkles (fig. 45). The flange of the protoconch projects above the caecum (fig. 44). A prismatic ridge occurs at the attachment of the proseptum to the protoconch wall (fig. 43).

The proseptum is a single prismatic structure. The second septum is nacreous and grows dorsally into the midheight of the prosepum toward the median plane (figs. 47, 49, 53, 57). Ventrally, however, the two septa are distinctly separated on the venter (figs. 47, 49, 53, 54, 56). This construction produces a relatively small second chamber composed of two wedge-forming sections on either side of the siphuncle (figs. 47, 49, 53).

These relationships are further clarified in



Figs. 16–21. *Baculites* sp. 16. *Baculites* sp. (AMNH 42905). View into the protoconch shows the proseptum (1), proseptal opening, and flange (F). The caecum and siphuncle are not preserved. 17. *Baculites* sp. (AMNH 42905). Close-up of the specimen in figure 16 reveals the flange (F), proseptum (1), and opening of the proseptum. A short necklike attachment (arrow) occurs at the opening of the proseptum. 18. *Baculites* sp. (AMNH 42905). Close-up of the proseptum (1) of the same specimen in figure 16 reveals wrinkles (upper arrow). A prismatic ridge occurs at the attachment of the proseptum to the wall of the protoconch (lower arrow). 19. *Baculites* sp. (AMNH 42905). Overview of the same specimen in figure 16 after most of the proseptum (1) has been removed reveals the short necklike attachment of the proseptum (arrow) adapical of the second septum (2). 20. *Baculites* sp. (AMNH 42905). The junction of the proseptum (1) and necklike attachment of the proseptum (arrow) magnified from figure 19 (white box). 21. *Baculites* sp. (AMNH 42906). Part of the proseptum (1) just below the flange (F) displays wrinkles.



Figs. 22–25. *Baculites* sp. 22. *Baculites* sp. (AMNH 42907). Lateral section through the protoconch and first whorl reveals the prosheptum (1), flange (F), and second septum (2). 23. *Baculites* sp. (AMNH 42907). More median section of the specimen in figure 22 shows the prosheptum (1), flange (F), and second septum (2). The necklike attachment (arrow) of the prosheptum begins to emerge. 24. *Baculites* sp. (AMNH 42907). Still more median section of the specimen in figure 22 shows the prosheptum (1), necklike attachment of the prosheptum (arrows), flange (F), and second septum (2). 25. *Baculites* sp. (YPM 6241). A median section through the protoconch and first whorl reveals the prosheptum (1), necklike attachment of the prosheptum (arrows), flange (F), and the second septum (2) with a well-developed prochoanitic septal neck.

more detailed views through the median plane. Dorsally, the second septum may appear as a rudiment below the prosheptum and

flange (figs. 51, 52, 58). Ventrally, however, it is a distinct structure a moderate distance from the prosheptum (figs. 48, 50, 51, 54–56,

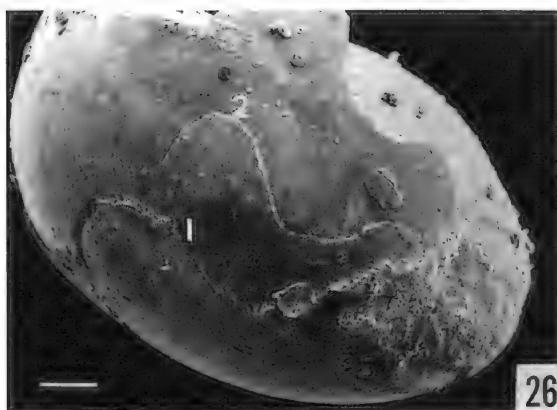


FIG. 26. *Baculites* sp. (AMNH 42908). Ventral view of the prosuture (1) and second suture (2) on a steinkern of the early whorls.

58). Prismatic deposits attach both septa to the siphuncle and caecum and form elongate grooves (figs. 48, 51, 52, 54, 55, 58). The third septum is separate from the second septum both ventrally and dorsally (fig. 50).

Muscle scars occur on the interior surface of the dorsal shell (fig. 46). The first scar occurs as a pair in the second chamber on either side of the prosopetal opening on the adoral face of the proseptum. The second scar is elongate and occurs in the third chamber above the siphuncle. The third and all subsequent scars are single and adoral of the dorsal lobes.

On steinkerns of the initial whorls, the prosuture and second suture are separated on the venter (fig. 59). The second suture displays shallow lateral lobes.

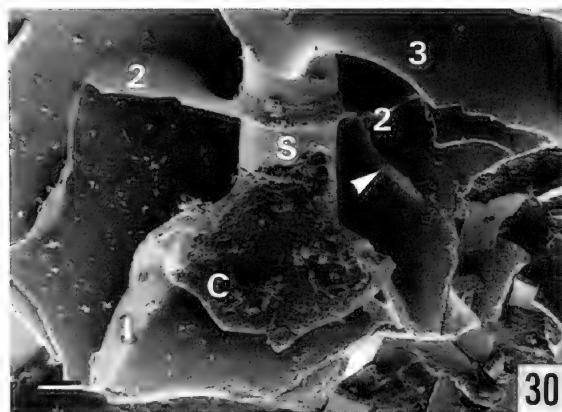
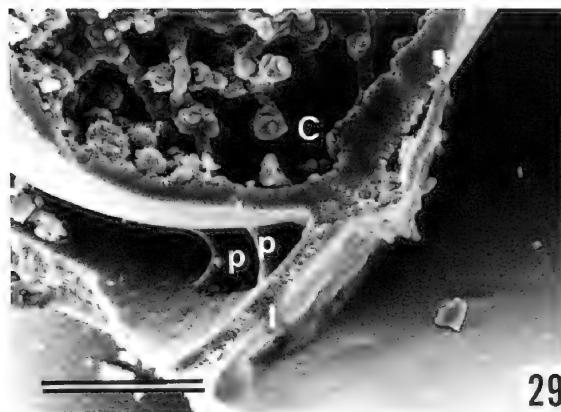
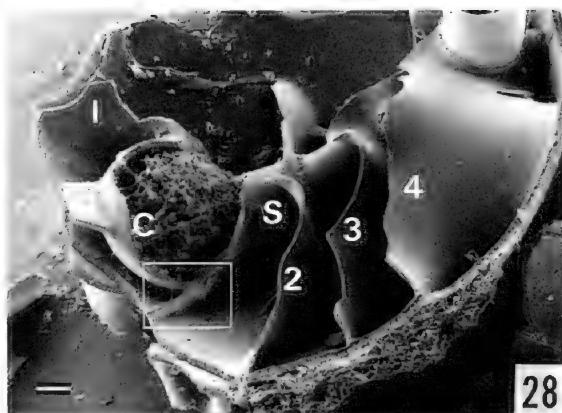
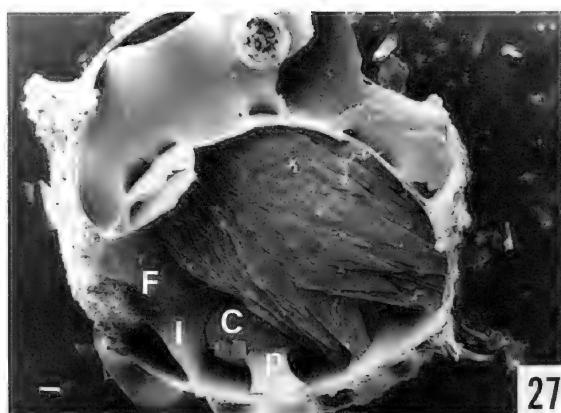
6. *Kosmoceras* (figs. 60–68). In protoconchs of this genus free of matrix we observe the caecum, flange, and first few septa (figs. 60, 61, 64, 65). The proseptum is a single structure. It is prismatic and displays a prismatic attachment to the caecum and siphuncle (figs. 66, 67). The second septum is nacreous and is separated from the proseptum both ventrally and dorsally (figs. 62, 63, 65). In one specimen the second septum forms a short adapical spur below the siphuncle (fig. 62). On steinkerns of the initial whorls, the ventral parts of the prosuture and second suture are distinctly separate (fig. 68). The lateral lobes of the second suture are more arched than those in *Quenstedtoceras*.

## DISCUSSION

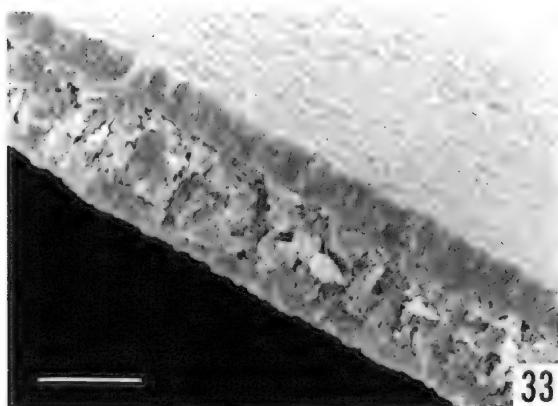
The internal features in all of the ammonites studied are basically very similar. The proseptum, or first septum, always develops at the transition from the cuplike protoconch into the planispiral first whorl (Erben, Flajs, and Siehl, 1969). It closes off the spherical to elliptical protoconch and appears to form a continuation of the flange. Its median portion consists of a circular opening whose diameter equals the whorl height. This opening is oriented in a nearly vertical position between the flange and outer shell wall. The proseptum joins the outer wall to form two lateral lobes and a median saddle.

In none of the genera studied did we observe two prosepta. In *Baculites* and in *Scaphites* and its allied genera, the proseptum is a single structure, although a necklike attachment surrounds the prosopetal opening. A single proseptum is also the rule in *Hypacanthoplites*, *Euhoplites*, *Kosmoceras*, and *Quenstedtoceras*. In *Quenstedtoceras*, the second septum grows dorsally into the proseptum and may appear in median section as a rudimentary structure on the dorsal part of the proseptum. This rudiment was previously described by Erben, Flajs, and Siehl (1969) and Bandel (1982), although Kulicki (1979) regarded it as a prismatic deposit of the proseptum.

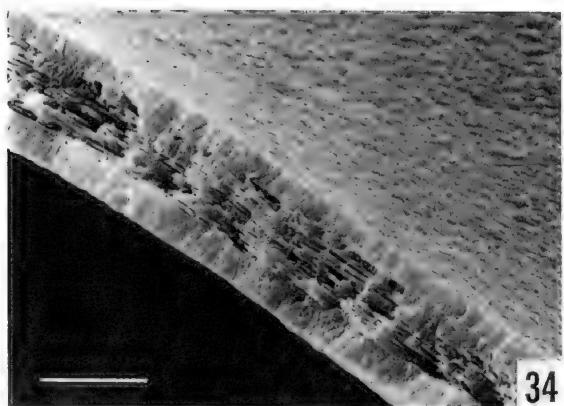
Prismatic attachment deposits are commonly developed around the openings of the first few septa and have previously been described in *Kosmoceras* by Kulicki (1979) and in *Quenstedtoceras* by Kulicki (1979) and Bandel (1982). In *Baculites* and in *Scaphites* and its allied genera an adorally directed necklike attachment also develops around the prosopetal opening in addition to the smaller prismatic deposits. The prismatic deposits attach the septa to the siphuncle and caecum and may form elongate grooves as shown in *Quenstedtoceras*. Bandel and Boletzky (1979) and Bandel (1982) have suggested that these prismatic deposits are implicated in the transfer of liquid from the chambers into the siphuncle. The caecum is attached to the protoconch by prosiphonal sheets displaying wrinkles. More finely divided attachments also occur between the caecum and the walls of the protoconch, as shown in *Euhoplites*.



Figs. 27-32. *Euhoplites* sp. (AMNH 27261a). 27. Interior of the protoconch shows the proseptum (1), flange (F), caecum (C), and prosiphon (p). 28. View of the specimen in figure 27 after much of the proseptum and dorsal wall has been removed reveals the caecum (C), siphuncle (S), and early septa (1, 2, 3, 4). The second septum (2) is distinct from the proseptum (1) both ventrally and dorsally. 29. Close-up of the proseptum (1) and caecum (C) from figure 28 (white box) reveals the delicate prosiphonal attachment strands (p) between the caecum (C) and protoconch wall. 30. View of the specimen in figure 28 after part of the caecum (C) has been removed. The second septum (2) is distinct from the proseptum (1) and displays a short adapical spur (arrow). 31. View of the dorsal shell of the specimen in figure 27 reveals muscle scars adoral of the proseptum (1) and the lobes of the next few septa (2, 3, 4). 32. Close-up of figure 31 suggests that the first scar actually consists of two separate but connecting scars.

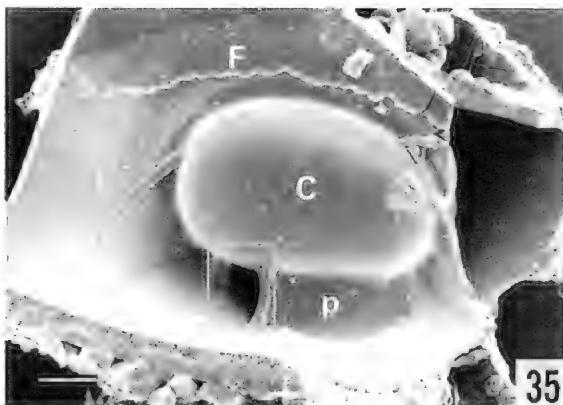


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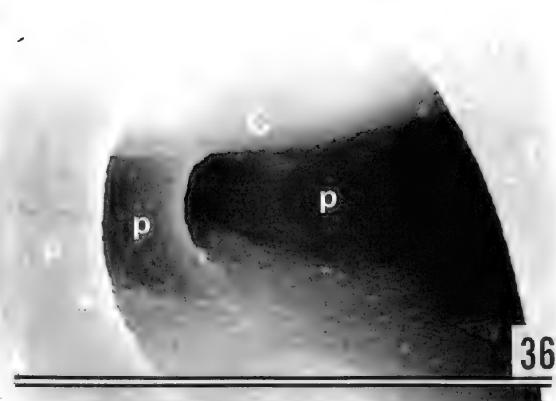


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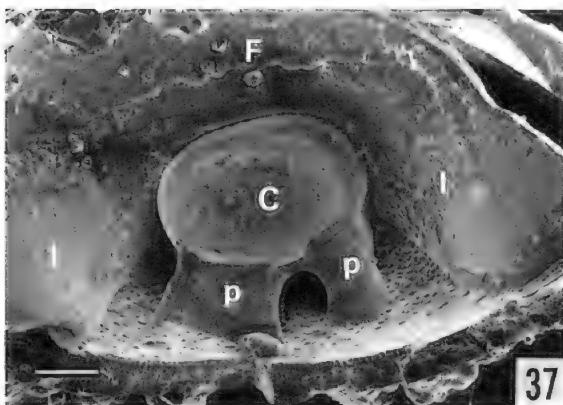
Figs. 33-34. *Euhoplites* sp. (AMNH 27261a) (scale bar 4  $\mu\text{m}$ ). 33. The prismatic layer of the proseptum is sandwiched between layers of a more homogeneous material which originally may have been organic. 34. The nacreous layer of the second septum is similarly sandwiched between layers of a more homogeneous material which originally may have been organic.



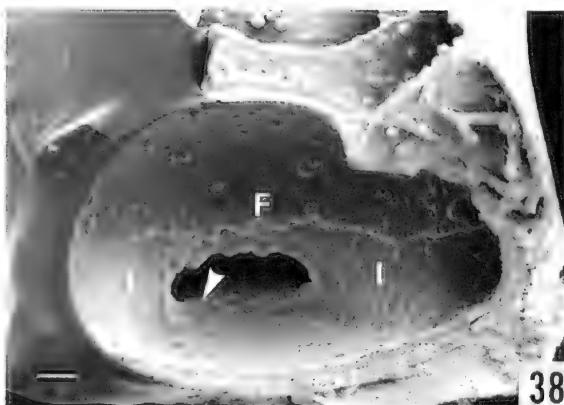
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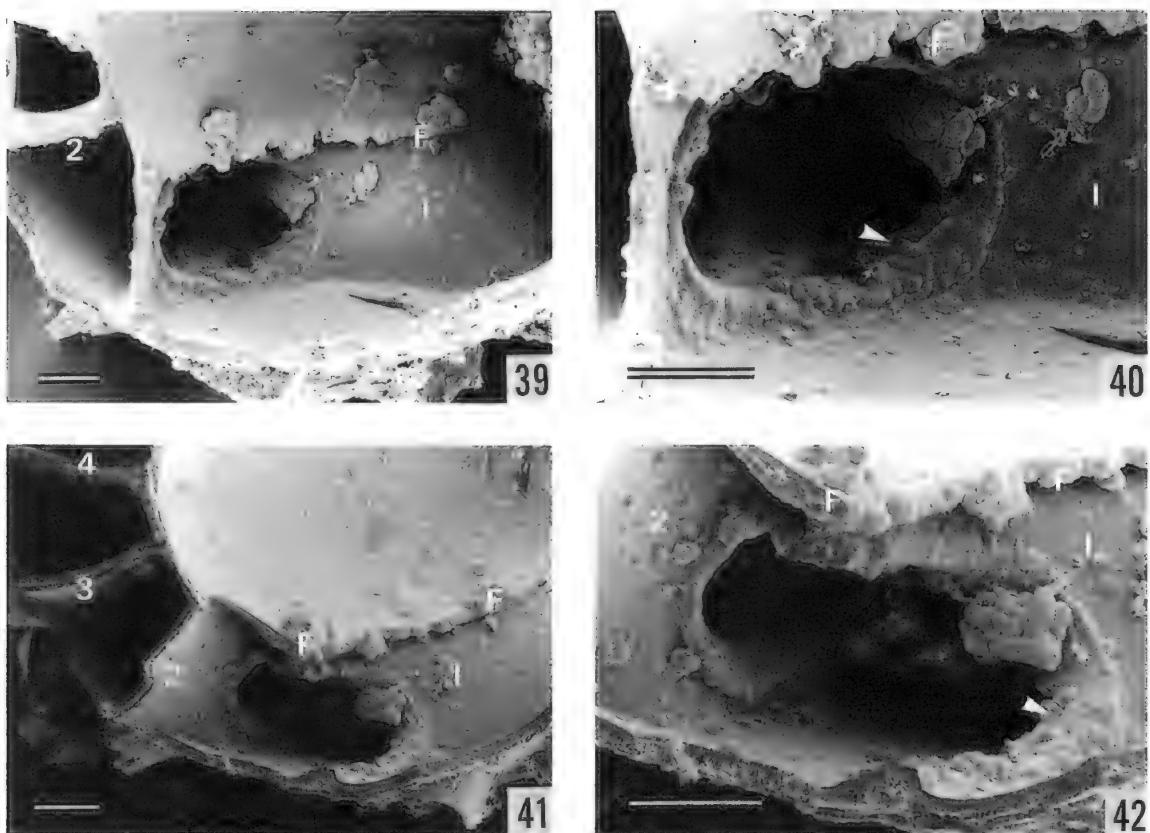


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Figs. 35-38. *Hypacanthoplites* sp. 35. *Hypacanthoplites* sp. (AMNH 20952a). Interior of the protoconch shows the caecum (C), prosiphon (p), proseptum (1), and flange (F). 36. *Hypacanthoplites* sp. (AMNH 20952a). Close-up of the specimen in figure 35 (white box) reveals minute prosiphonal attachments (p) between the caecum (C) and protoconch wall. 37. *Hypacanthoplites* sp. (AMNH 20952b). Interior of the protoconch with the caecum (C), prosiphon (p), proseptum (1), and flange (F). 38. *Hypacanthoplites* sp. (AMNH 20952c). Interior of the protoconch shows the flange (F) and proseptum (1). A furrow or short necklike attachment (arrow) occurs around the opening of the proseptum.



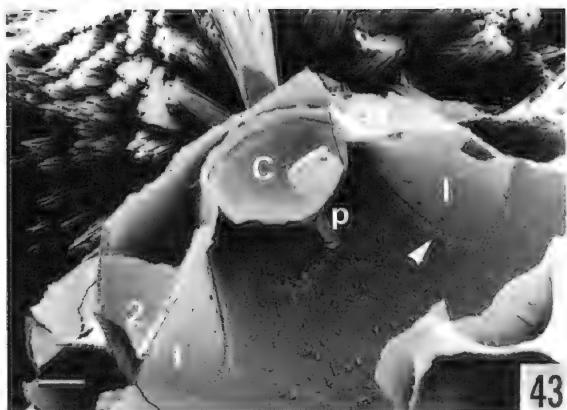
Figs. 39–42. *Hypacanthoplites* sp. (AMNH 20952d). 39. View into the interior of the protoconch reveals the proseptum (1), flange (F), and second septum (2). The caecum is not preserved. 40. Close-up of the specimen in figure 39 shows the flange (F) and proseptum (1). A furrow or short necklike attachment (arrow) occurs around the opening of the proseptum. 41. Same specimen in figure 39 with part of the proseptum (1) removed reveals the flange (F), second (2), third (3), and fourth (4) septa. 42. Close-up of figure 41 shows the proseptum (1), opening of the proseptum with its furrow (arrow), flange (F), and the second septum (2) and its opening.

and *Hyacanthoplites*, and have previously been called partial septa by Shimizu (1929) and Tanabe et al. (1979).

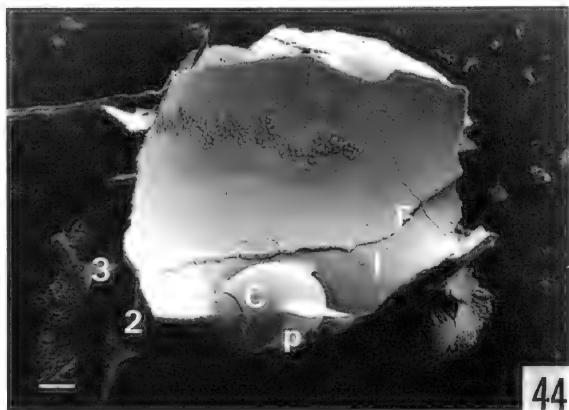
The microstructure of the proseptum and second septum was observed in all genera except *Hypacanthoplites*. In *Quenstedtoceras* and *Kosmoceras* the proseptum is prismatic and the second septum is nacreous, as previously documented by Kulicki (1979) and Bandel (1982). Similarly, in *Scaphites* and its allied genera the proseptum is prismatic and the second septum is nacreous as suggested by Birkelund and Hansen (1974) in contrast to Erben, Flajs, and Siehl (1969). Finally, in *Baculites*, as previously shown by Landman

(1982b), and in *Euhoplites*, the first septum is prismatic and the second septum is nacreous.

These detailed observations on the microstructure of the first two septa necessitate a revision in the terminology used to describe them. The term proseptum emphasizes the uniqueness of the first septum compared to all later septa. However, the second and third septa are commonly called the primary septum and nacreoseptum, respectively; this implies that the first nacreous septum is the third septum. Our observations indicate, to the contrary, however, that in all genera studied nacre is already developed by the second sep-



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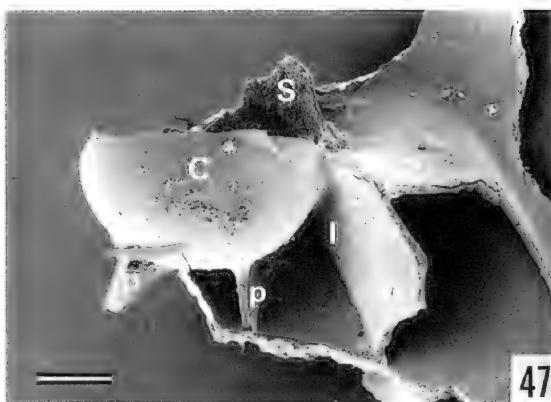
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Figs. 43–46. *Quenstedtoceras* sp. 43. *Quenstedtoceras* sp. (AMNH 42909). Interior of the protoconch with the caecum (C), part of the prosiphon (p), proseptum (1), and second septum (2). A prismatic ridge (arrow) occurs at the attachment of the proseptum to the wall of the protoconch. 44. *Quenstedtoceras* sp. (AMNH 42910). View of the caecum (C), prosiphon (p), flange (F), proseptum (1), and second (2) and third (3) septa. 45. *Quenstedtoceras* sp. (AMNH 42911). Caecum (C) and prosiphon (p) of the specimen in figure 49. 46. *Quenstedtoceras* sp. (AMNH 42910). View of the dorsal shell of the specimen in figure 44 reveals the muscle scars adoral of each of the first three septa. The first set of muscle scars (arrow) occurs as a pair (only one showing) on either side of the opening on the adoral face of the proseptum (1). The second set of scars also occurs as a pair adoral of the second septum (2). The third set occurs as a single scar adoral of the third septum (3). Note how the second septum grows into the opening of the proseptum.

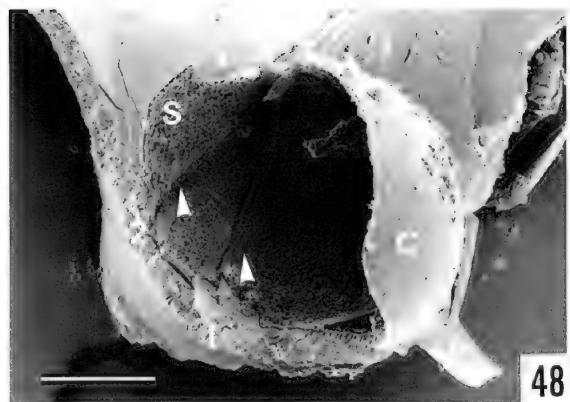
tum. Therefore, in agreement with Drushchits and Khiami (1970), we recommend that the terms primary septum and nacooseptum be replaced by the simpler terms second and third septa.

Finally, the spatial relationship between the first two septa was studied in all ten genera. In *Kosmoceras*, the second septum is a moderate distance from the proseptum and, as shown by Kulicki (1979), is convex toward the aperture in median section. In *Baculites*,

the second septum is similarly distant from the proseptum except near the extreme lateral margins and is convex toward the aperture in median section. The first two septa are also moderately far apart in *Euhoplites* and *Hypacanthoplites*. In *Scaphites* and related genera, the second septum is again separate from the proseptum and, in median section, convex toward the aperture. The first two septa only intersect on the extreme lateral margins. However, in *Quenstedtoceras*, the second

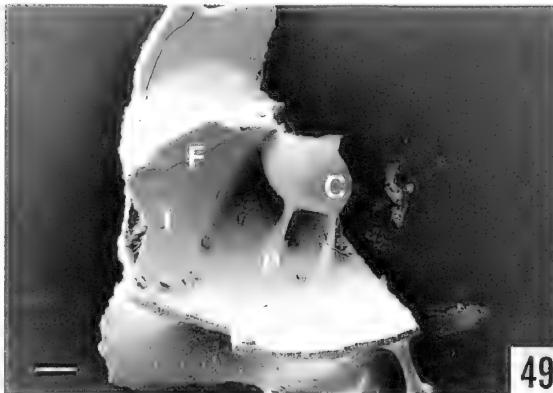


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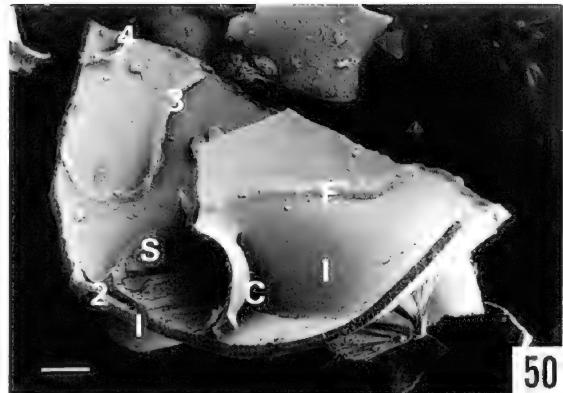


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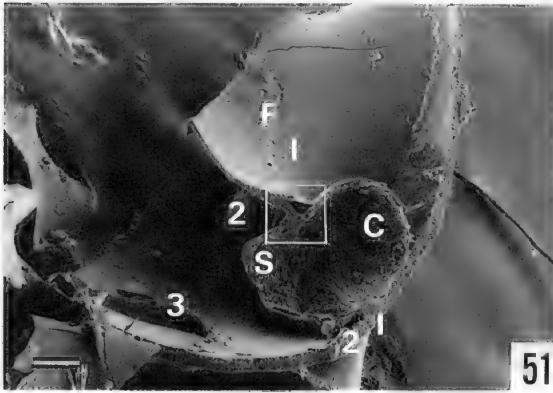
Figs. 47–48. *Quenstedtoceras* sp. (AMNH 42912). 47. View of the caecum (C), siphuncle (S), prosiphon (p), proseptum (1), and second septum (2). The second septum grows dorsally into the proseptum toward the median plane. 48. Another view of the specimen in figure 47 looking into the caecum (C) reveals parts of the siphuncle (S), prosiphon (p), proseptum (1), and second septum (2). The prismatic attachment deposits of the siphuncle and caecum (arrows) are associated with grooves.



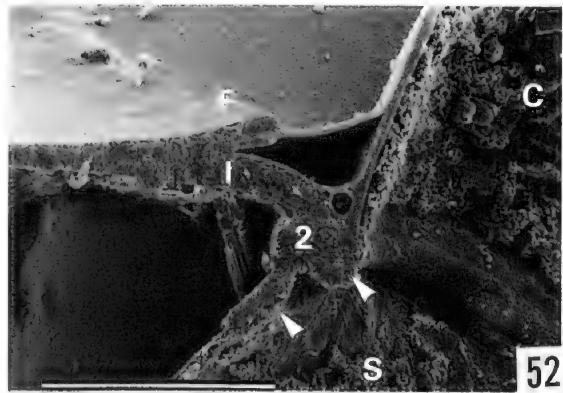
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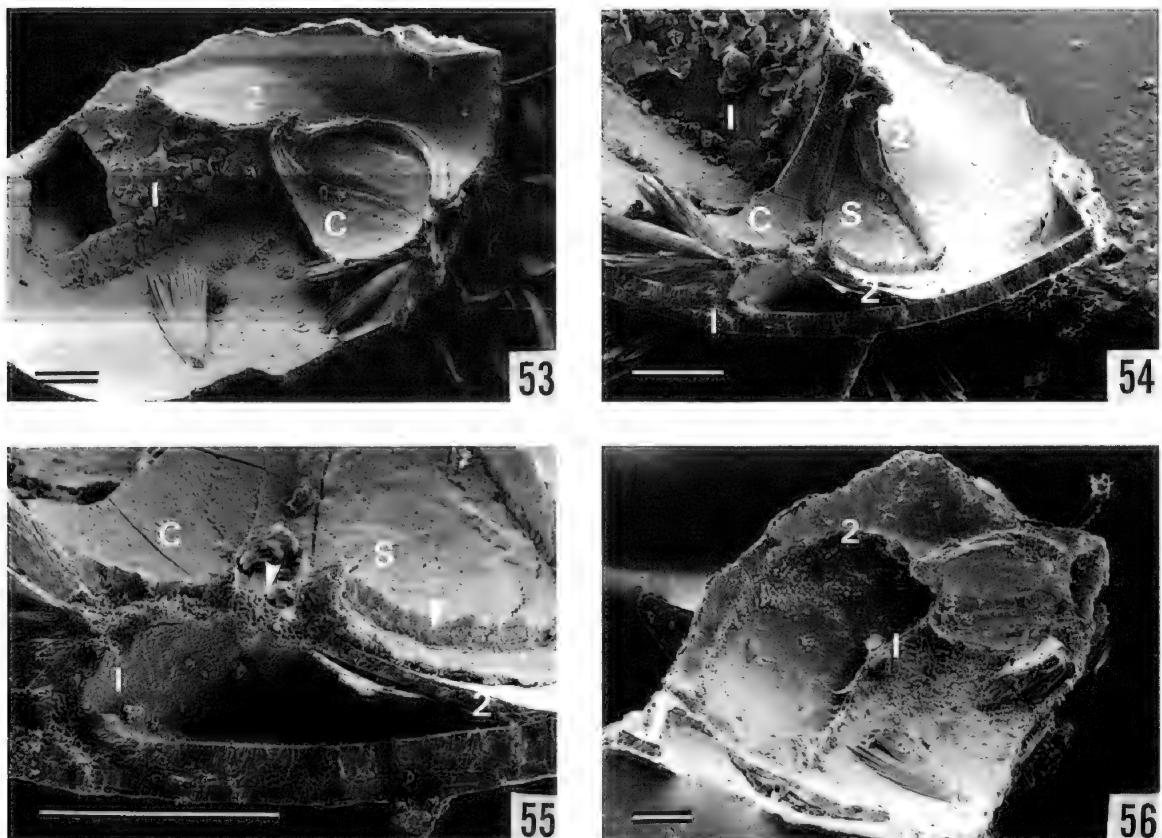


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Figs. 49–52. *Quenstedtoceras* sp. (AMNH 42911). 49. Interior of the protoconch with the caecum (C), prosiphon (p), proseptum (1), flange (F), and second septum (2). 50. The other half of the specimen in figure 49 shows the caecum (C), part of the siphuncle (S), flange (F), proseptum (1), part of the second septum (2), and ventral traces of the third (3) and fourth (4) septa. 51. Specimen in figure 50 slightly rotated to reveal the interior of the caecum (C), parts of the siphuncle (S), proseptum (1), flange (F), and the second (2) and third septa (3). 52. Close-up of figure 51 (white box) shows the caecum (C), siphuncle (S), flange (F), proseptum (1), possible rudiment of the second septum (2), and prismatic attachment deposits of the siphuncle and caecum (arrows).

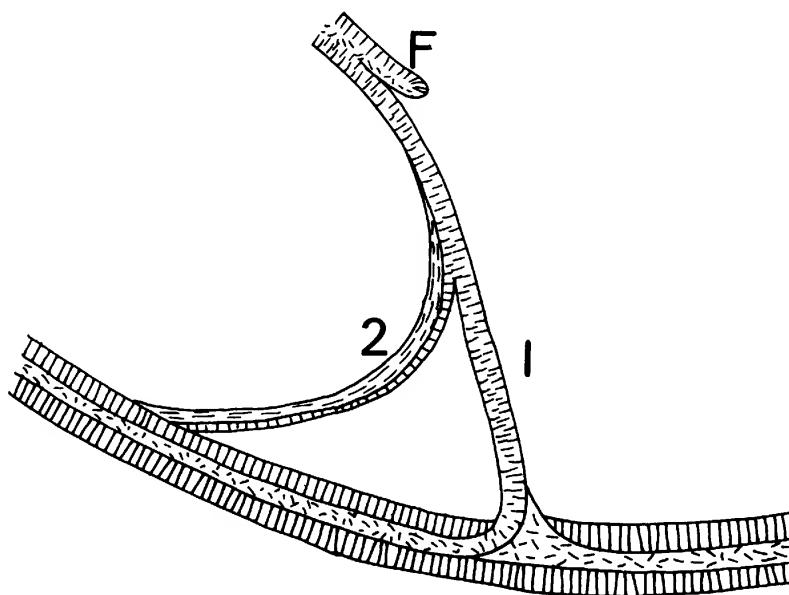


Figs. 53–56. *Quenstedtoceras* sp. (AMNH 42913). 53. Interior of the protoconch with the proseptum (1), second septum (2), and part of the caecum (C). 54. Magnified view of the specimen in figure 53 from the right shows the proseptum (1), second septum (2), part of the caecum (C), and siphuncle (S). 55. Close-up of figure 54 reveals the proseptum (1), second septum (2), and parts of the caecum (C) and siphuncle (S) and their prismatic attachment deposits (arrows). 56. The same view as in figure 53 with the proseptum (1) and second septum (2) leveled flat reveals that the first two septa are distinct on the venter.

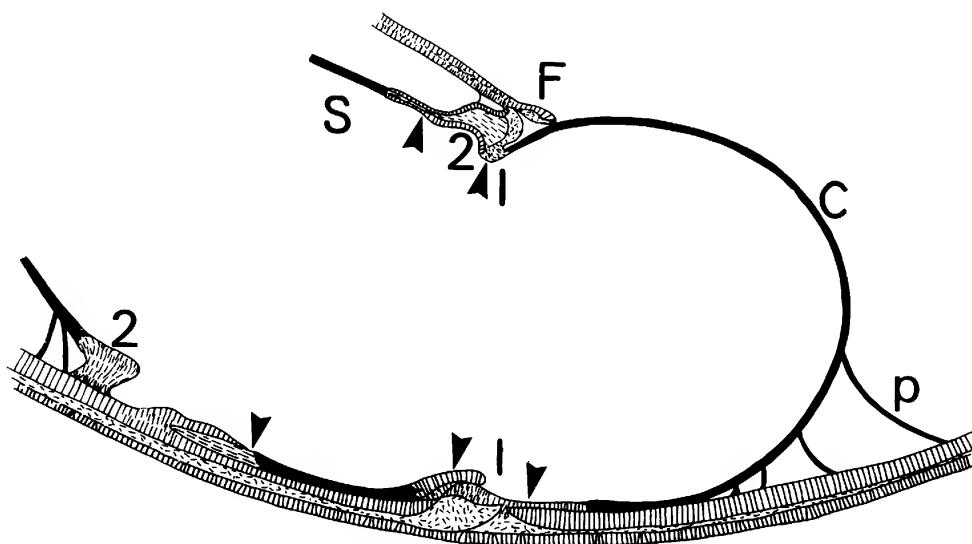
septum rides dorsally on the proseptum, as previously shown by Drushchits and Khiami (1970), Kulicki (1979), and Bandel (1982), although ventrally the two septa are distinct. A similar construction has been observed in the closely related genus *Cadoceras* (Drushchits, Doguzhayeva, and Lominadze, 1977).

These spatial relationships are also expressed in the spacing of the corresponding sutures on steinkerns of the initial whorls. In *Kosmoceras*, *Quenstedtoceras*, *Baculites*, and *Scaphites* and related genera the second suture is ventrally separate from the prosuture. It consists of a median lobe and lateral saddles. Dorsally, the first two sutures are distinct except in *Quenstedtoceras*.

A general model outlining the early ontogenetic development of ammonites was proposed by Bandel (1982) and is supported by several of our observations. According to this model, the visceral mass first differentiated to form the cells of the siphuncle and, subsequently, the ammonite began construction of its phragmocone. The visceral mass withdrew from the protoconch but was still attached to it by retractor muscles and siphuncular tissue. The retractor muscles were probably attached to the inner side of the flange and the siphuncular tissue to the wall of the protoconch. The visceral mass formed an organic sheet with a central opening to accommodate the siphuncle and muscles.



57



58

Figs. 57-58. *Quenstedtoceras* sp. Diagrams of serial sections prepared parallel to the median plane reproduced from Bandel (1982). 57. A lateral section through the protoconch and first whorl shows the proseptum (1), second septum (2), and flange (F). 58. A median section shows the caecum (C), prosiphon (p), siphuncle (S), flange (F), proseptum (1), second septum (2), and prismatic attachment deposits of the siphuncle and caecum (arrows).

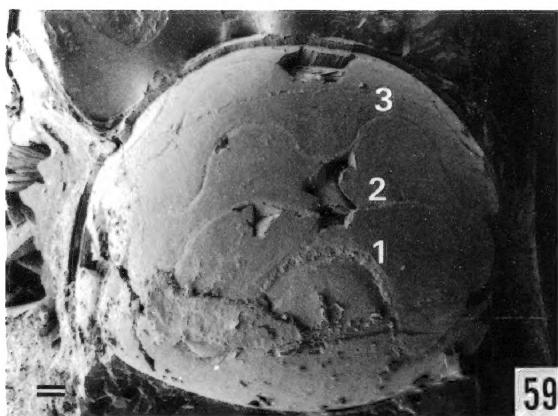
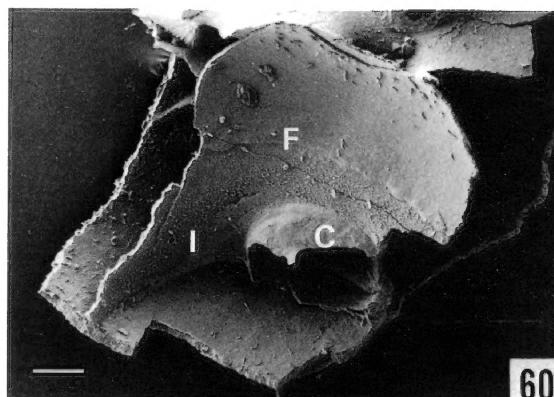


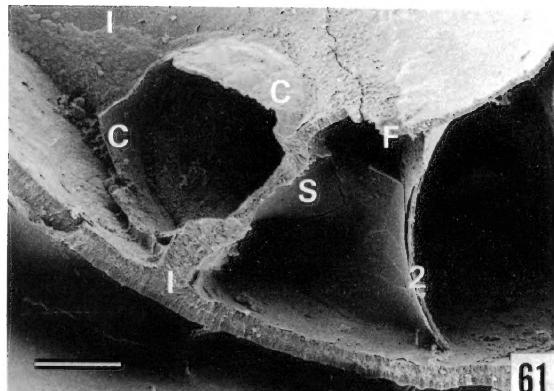
FIG. 59. *Quenstedtoceras* sp. (AMNH 42914). Ventral view of the prosuture (1), second suture (2), and third suture (3) on a steinkern of the early whorls.

This organic precursor of the proseptum was firmly attached to the walls of the protoconch in a prismatic ridge as shown in *Baculites*, *Scaphites*, *Quenstedtoceras*, and *Kosmoceras*. It later mineralized, wrinkles and all, to form the prismatic proseptum as shown, for example, in *Baculites*.

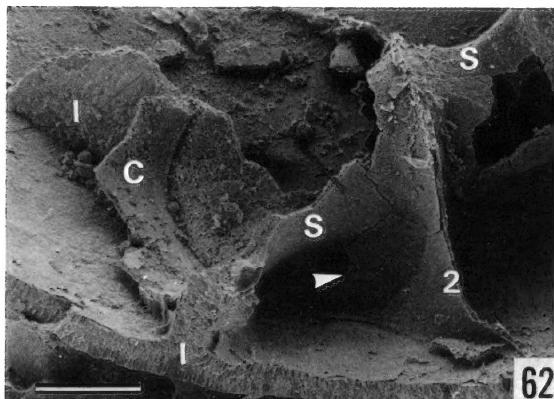
After formation of the proseptum, the retractor muscles reattached in two bundles to the adoral face of the proseptum on either side of the proseptal opening as shown in *Euhoplites* and *Quenstedtoceras*. Subsequently, the caecum and its prosiphonal attachment sheets formed. At this stage of development, the ammonite hatched from its



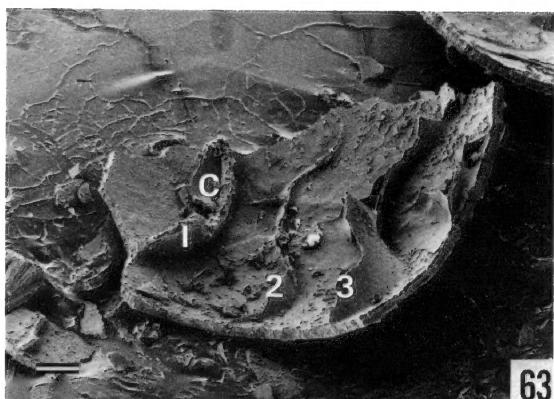
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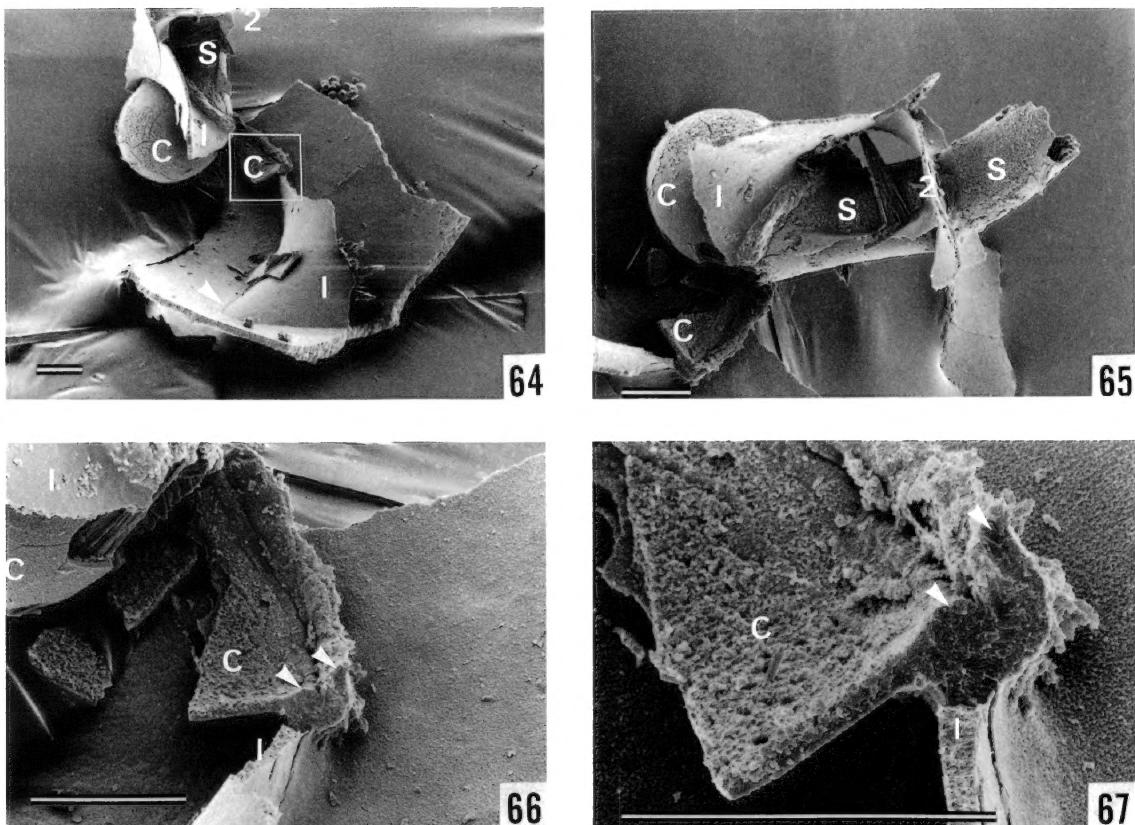


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FIGS. 60-63. *Kosmoceras* sp. (AMNH 42915). 60. Interior of the protoconch with the proseptum (1), flange (F), and part of the caecum (C). 61. Specimen in figure 60 viewed from a slightly different angle shows the proseptum (1), flange (F), caecum (C), siphuncle (S), and second septum (2). 62. Same view as in figure 61 after parts of the proseptum (1) and caecum (C) have been removed reveals that the second septum (2) is distinctly separated from the proseptum. Note the adapical spur (arrow) below the siphuncle (S). 63. Specimen in figures 60-62 after most of the shell has been removed shows that the first three septa are distinct on the venter.



Figs. 64–67. *Kosmoceras* sp. (AMNH 42916). 64. Interior of part of the protoconch and first whorl with the prosheptum (1), caecum (C), siphuncle (S), and second septum (2). A prismatic ridge (arrow) occurs at the attachment of the prosheptum. 65. Specimen in figure 64 viewed at a slightly different angle shows the prosheptum (1), caecum (C), siphuncle (S), and second septum (2). The second septum is distinctly separated from the prosheptum. 66. Close-up of figure 64 (white box) reveals the prosheptum (1), caecum (C), and prismatic attachment deposits of the caecum and siphuncle (arrows) and their associated groove. 67. Close-up of figure 66 plainly shows the prosheptum (1), caecum (C), and the prismatic attachment deposits of the caecum and siphuncle (arrows) and their associated groove.



FIG. 68. *Kosmoceras* sp. (AMNH 42917). Ventral view of the prosuture (1), second suture (2), and third suture (3) on a steinkern of the early whorls.

egg capsule as a miniature adult with the capability to control buoyancy. It could fully or partly pump out liquid from its protoconch and utilize the resultant lift.

#### ACKNOWLEDGMENTS

We thank Dr. Edwin Kemper who kindly identified the specimens of *Hypacanthoplites* and Drs. Tove Birkelund, Harry Mutvei, Cyprian Kulicki, Niles Eldredge, and John Maisey who critically reviewed the manuscript. Misses Joan Whelan and Eileen Polk assisted in scanning electron microscopy, Mr. Peter J. Harries in photography and plate preparation, and Miss Susan Klofak in specimen preparation.

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